Systematic leaf anatomy of selected genera of southern African Alooideae (Asphodelaceae)

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Leaf anatomical features were studied in the taxonomically controversial Alooideae genera, *Chortolirion* Berger and *Poellnitzia* Uitewaal (both monotypic), as well as the aberrant *Aloe bowiea* Schult. & J.H. Schult. [= *Chamaealoe africana* (Haw.) Berger]. Particular reference is made to the taxonomic significance of epidermal characters in the subfamily. Previous claims that leaf cuticular sculpturing is under strong genetic control, and thus rather invariant, are contradicted by some infraspecific variation in patterning observed in at least *Chortolirion* and *Aloe bowiea*. Anatomical characters diagnostic for a particular genus were nevertheless evident in all samples of a species. Furthermore, scanning electron microscopic studies of both leaf surfaces proved to be invaluable in assessing variation patterns. Of particular taxonomic significance are the distribution and structure of the vascular bundles (presence/absence of enlarged parenchymatous cells in the inner bundle sheath), presence of palisade cells and location of crystalliferous idioblasts. Leaf anatomical data support the maintenance of *Chortolirion* and *Poellnitzia* as distinct genera, whereas *Aloe bowiea* falls within the range of variation previously reported for the genus *Aloe*.

Blaaranatomiese kenmerke is ondersoek in die twee taksonomies kontroversiële Alooideae-genusse, *Chortolirion* Berger en *Poellnitzia* Uitewaal, sowel as die afwykende *Aloe bowiea* Schult. & J.H. Schult. [= *Chamaealoe africana* (Haw.) Berger]. Aandag word veral geskenk aan die taksonomiese nut van epidermale kenmerke in die subfamilie. Vorige beweringe dat blaarkutikulaskulptuur geneties streng beheer word, en dus min varieer, is teenstrydig met 'n mate van intraspesifieke variasie wat wel in die geval van ten minste *Chortolirion* en *Aloe bowiea* waargeneem is. Anatomiese kenmerke wat diagnosties is vir 'n bepaalde genus, is nietemin in alle eksemplare van 'n spesie waargeneem. Verder is skandeerelektronmikroskopiese ondersoeke van beide blaaroppervlaktes wenslik om sodoende die variasie in patrone teenwoordig by 'n spesie, vas te stel. Veral die verspreiding en bou van die vaatbondels (teenwoordigheid/afwesigheid van vergrote parenkiemagtige selle in die binneste bondelskede), teenwoordigheid van palissadeselle, en die ligging van kristalhoudende idioblaste is van besondere taksonomiese belang. Blaaranatomiese data verleen steun aan die behoud van *Chortolirion* en *Poellnitzia* as afsonderlike genusse, terwyl die blaaranatomie van *Aloe bowiea* binne die bestek van variasie val wat voorheen vir die genus vermeld is.

Keywords: *Aloe*, anatomy, *Chamaealoe, Chortolirion,* epidermis, leaf, *Poellnitzia*, taxonomy.

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Introduction

Following a recent survey of relationships among alooid taxa (Smith & Van Wyk 1991), the subfamily Alooideae, Asphodelaceae (*sensu* Dahlgren *et al.* 1985) is considered to comprise seven genera. With the exception of the Mascarene and Madagascan *Lomatophyllum* Willd., all of these are strongly represented within the *Flora of Southern Africa* region. Previous anatomical research in this group, mainly by Dr D.F. Cutler and co-workers of the Jodrell Laboratory, Royal Botanic Gardens, Kew, have involved mainly the principal genera, *Aloe* L., *Gasteria* Duval and *Haworthia* Duval. Initiated more than 20 years ago, the latter, continuing research programme has concentrated on, amongst others, studies on the range of leaf epidermal patterns in the subfamily Alooideae (Brandham & Cutler 1978, 1981). This has revealed that leaf surfaces show a range of cell arrangement, stomatal structure and cuticular sculpturing which, when taken together, are frequently diagnostic for a species or group of closely related species (Cutler 1982; Carter *et al.* 1984; see also Frölich & Barthlott 1988 on epicuticular waxes of monocotyledons).

Furthermore, previous studies on the Alooideae have demonstrated that aspects such as epidermal cell patterns, stomatal structure as seen on leaf surfaces and even patterns of leaf pigmentation are under strong genetical control in at least some members of the group (Cutler 1972, 1978a; Brandham 1977; Cutler & Brandham 1977; Cutler *et al.* 1980). Epidermal surface patterns, in particular, proved to be sufficiently stable and taxon-specific (Cutler 1969, 1972), thus providing useful taxonomic characters which may aid in the identification of, especially, non-flowering alooid plants (Glen & Hardy 1986).

As part of the wider leaf anatomical study of the Alooideae currently under way, the following southern African species are being examined: *Aloe bowiea* Schult. & J.H. Schult., *Chortolirion angolense* (Bak.) Berger and *Poellnitzia rubriflora* (L. Bol.) Uitewaal. *Chortolirion* Berger and *Poellnitzia* Uitewaal are here considered to be monotypic genera. The third species, *A. bowiea*, was previously regarded as the only constituent of *Chamaealoe* Berger, a

genus now included in the synonymy of *Aloe* (Smith 1990). The leaf anatomy of these three taxa is presented and its usefulness for diagnostic or taxonomic purposes is considered.

Materials and Methods

Leaf material of all the species was obtained from plants collected in the field and subsequently grown under uniform conditions. As shown previously by Cutler (1978a), glasshouse-grown plants retain their epidermal features unaltered when compared with samples collected from plants in the wild. Fully expanded leaves were freshly collected, fixed and stored in formalin–acetic acid–alcohol (FAA) (Johansen 1940). All leaves were examined at a standard level, halfway between the base and apex. Voucher specimens and locality details pertaining to the various samples studied are listed in Table 1.

For light microscopy (LM), small portions of fixed material were dehydrated, infiltrated and embedded according to standard methods in glycol methacrylate (GMA) (Feder & O'Brien 1968). Transverse sections, 1 – 3 μm thick, were stained with the periodic acid/Schiff's (PAS) reaction, counterstained with toluidine blue (TB) and mounted in Entellan (Feder & O'Brien 1968). For the detection of calcium oxalate crystals, sections were stained with TB and viewed under polarized light. Cuticular preparations were obtained after treatment with Jeffreys' solution, and stained with safranin O (Kiger 1971). To elucidate epidermal cell shape and stomatal structure further, paradermal free-hand sections were prepared and stained with TB or safranin O.

Standard procedures were followed for scanning electron microscopic (SEM) studies of both adaxial and abaxial leaf surfaces. Leaf tissue fixed in FAA was infiltrated with liquid CO_2 and dried in a critical-point drier, sputter-coated with gold and viewed with the SEM.

Unless otherwise indicated, the descriptive terminology with regard to epidermal structure proposed for the Alooideae by Cutler and co-workers (Cutler 1982 and references cited therein) is used. Descriptors to indicate abundance and frequency are based on those proposed by Schmid (1982).

Table 1 Origin of material and list of voucher specimens[a]

Species	Locality number	Locality, grid reference	Collection number	Figure
Aloe bowiea	1	Brakfontein, Kariega; 3325 AC Port Elizabeth	206	11B
	2	Maasward, Coega; 3325 DC Port Elizabeth	173	1B, 2, 5 8, 11A, 12
	3	Jachtvlakte, Uitenhage; 3325 CD Port Elizabeth	1 (PEU)	—
Poellnitzia rubriflora	4	Langverwacht; 3320 CC Montagu	176	7
	5	Sandberg, Robertson; 3319 DD Robertson	184	10
	6	5 km W of Bonnievale; 3320 CC Montagu	9 (PRU)	1C, 4, 15, 16
Chortolirion angolense	7	Cachet railway siding; 2627 CA Potchefstroom	14	1A, 3, 6, 9, 13, 14

[a] All collection numbers are those of the first author. Unless otherwise indicated all specimens are deposited in PUC. One specimen from each locality was studied.

Results

The general distribution of tissues in the leaf is rather similar to that described for other alooid genera (Figure 1). However, there are several differences and it is mainly some of these features which will be considered. A summary of the main leaf anatomical differences between the investigated species is given in Table 2. More detailed descriptions follow below.

Aloe bowiea (Figures 1B, 2, 5, 8, 11 and 12)

Leaf in transverse section, LM

Outline crescentiform with a shallow mid-adaxial groove; margins rounded, with scattered prickles. *Cuticle* relatively thin (*ca.* 3 μm), following outline of outer wall of epidermal cells; outer part clear, inner part apparently grading with cutinized outer-most part of epidermal cell wall. Lobes forming the suprastomatal cavity well developed, consisting in part of an extension of the wall of the subsidiary cell. *Epidermal cells* usually slightly periclinally elongated (rectangular); those on both surfaces similar. Outer periclinal walls moderately cutinized (6 μm thick). *Stomata* sunken, suprastomatal cavity with parallel or slightly overarching lobes. Guard cell walls slightly and evenly thickened; cuticular ledges bordering outer and inner pore very short and apparently containing some cell wall material (they stained dark pinkish purple with PAS/TB). *Hypodermis* absent. *Chlorenchyma* several-layered; cells thin-walled; present to inner sides of both surfaces, as well as the margins; cells of 1 – 3 outermost layer(s) slightly and irregularly radially elongated, but not distinctly palisade-like; those of inner layers more or less isodiametric. *Vascular bundles* arranged more or less equidistant from leaf surface at boundary between chlorenchyma and central parenchymatous water storage tissue; more numerous (*ca.* 12) abaxially than adaxially (*ca.* 5); bundles of roughly equal size; phloem poles directed outwards; no bundles distinctly positioned as groove or marginal ones (Figure 1B). *Phloem pole* more or less T-shaped in outline, the stalk of the T directed outwards. Sieve tubes and companion cells very narrow. *Xylem* composed of few (2 – 6) tracheids of medium width. *Bundle sheaths* consisting of two layers of parenchyma cells; outer layer sometimes difficult to distinguish from surrounding cells; inner layer forming a conspicuous cap of large, thin-walled cells at the phloem pole; sectional area of cap larger than that of phloem and xylem together. *Sclerenchyma* absent. *Central tissue* composed of large parenchymatous cells; more or less sharply demarcated from chlorenchyma. *Crystals* present as raphide bundles in idioblasts; scattered amongst chlorenchyma cells, but not specifically associated with vascular bundles. *Silica bodies* and *tannins* not observed.

Leaf epidermis/surface, LM & SEM

Stomata anomocytic, sunken; lobes nearly upright, fused; outer pore more or less square, occasionally longer than wide. *Primary sculpturing*: epidermal cells mostly 5- or 6-sided; as long as wide, or slightly longer; anticlinal walls

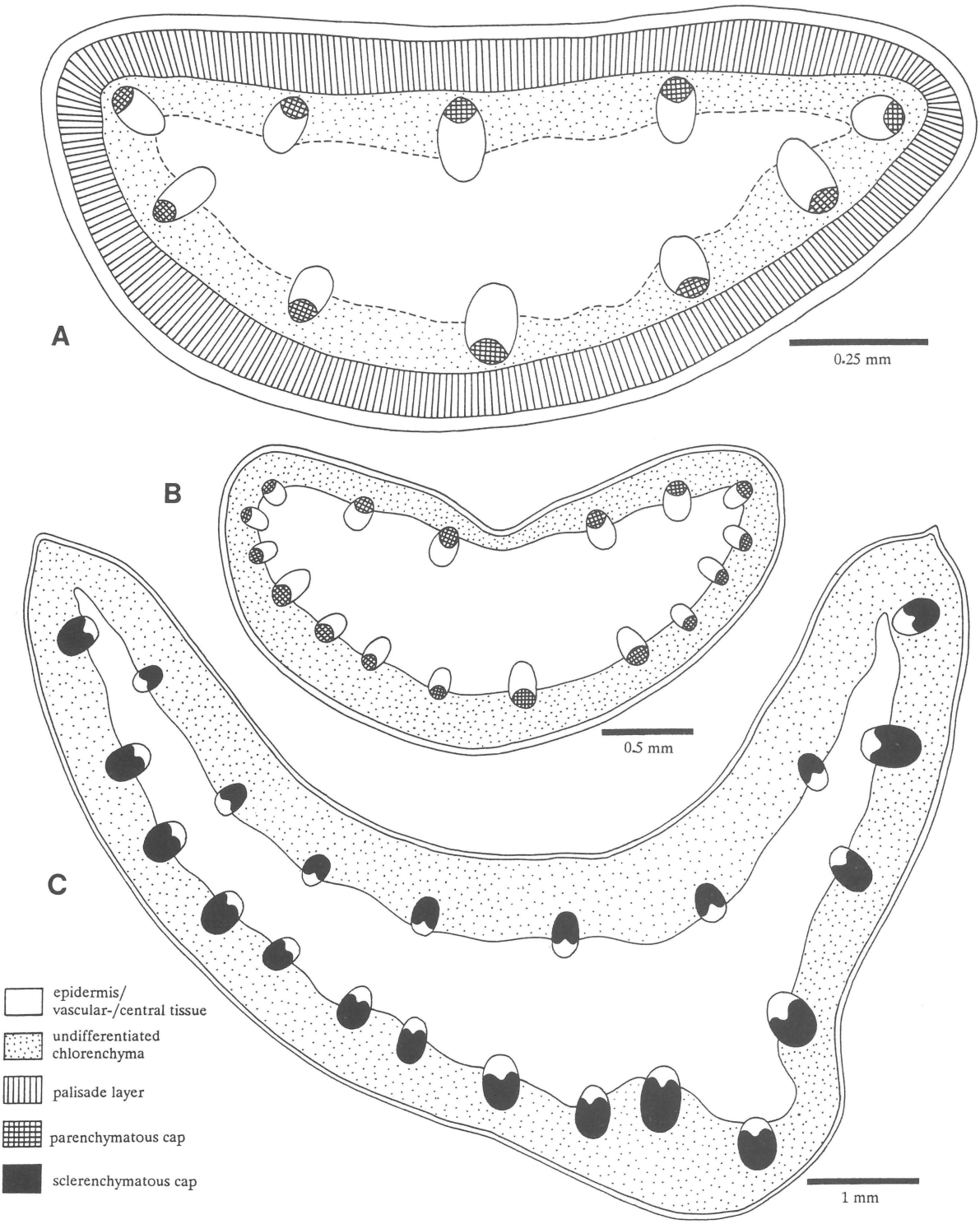


Figure 1 Diagrammatic representation of transverse sections of leaves illustrating distribution of tissues in *Chortolirion angolense* (A), *Aloe bowiea* (B) and *Poellnitzia rubriflora* (C). Sources of material are given in Table 1.

indistinct or only slightly depressed. *Secondary sculpturing:* outer periclinal walls of epidermal cells slightly convex; papillae generally absent; a single centrally positioned papilla present on most cells on the abaxial surface of the Kariega collection only (Figure 11B). *Tertiary sculpturing*: micropapillae moderately coarse, many per cell, distributed over entire surface of each cell; those on subsidiary cells more prominent. *Wax* present as amorphous deposits over entire leaf surface, partly blocking some stomata.

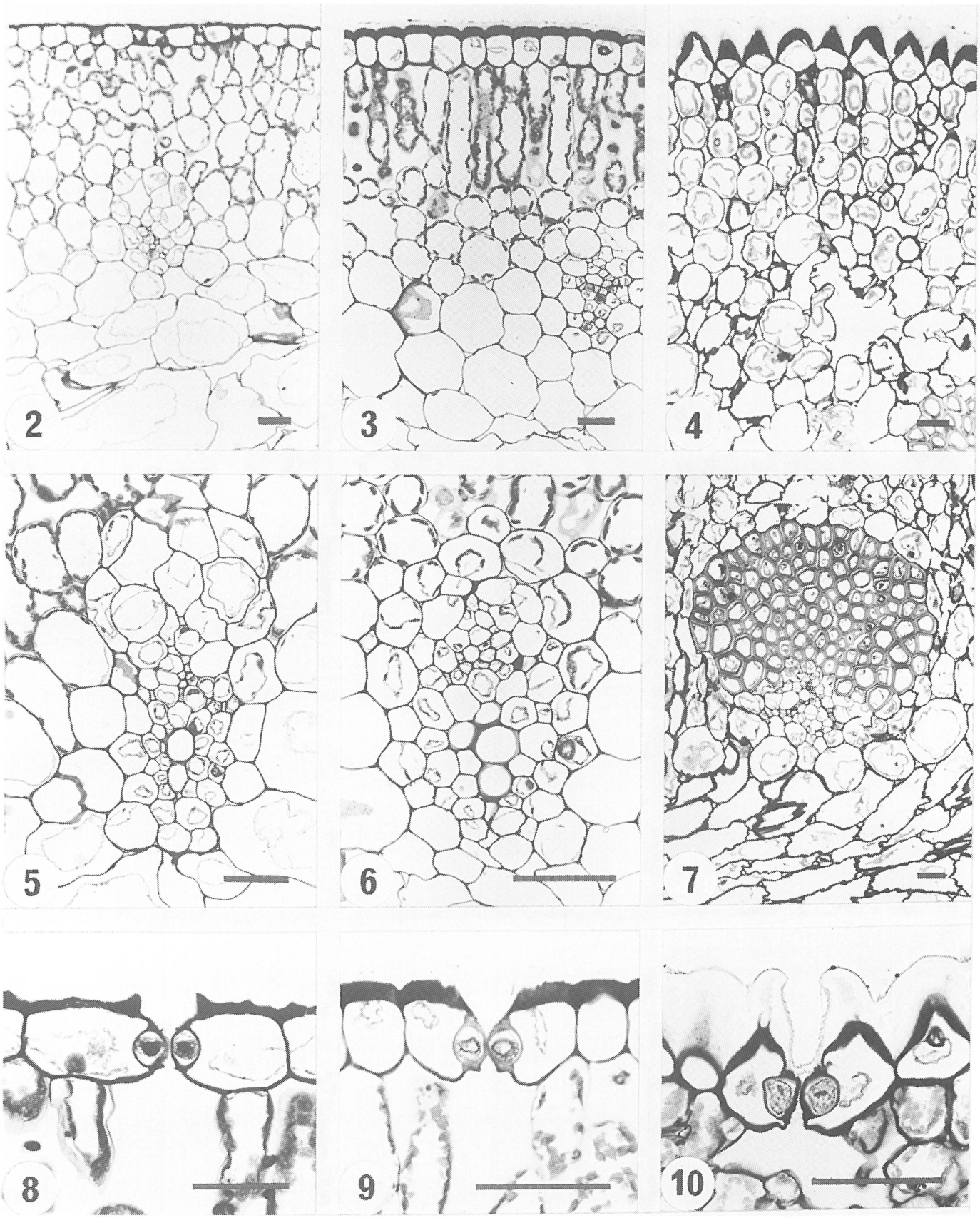
Chortolirion angolense (Figures 1A, 3, 6, 9, 13 and 14)

Leaf in transverse section, LM

Outline broadly triangular (plano-convex) in transverse section; adaxial surface more or less plane; abaxial surface convex; margins rounded, with scattered prickles. *Cuticle* relatively thin (up to 8 μm), following outline of outer wall of epidermal cells, clear. Lobes forming the suprastomatal cavity well developed, without subsidiary cell wall extensions. *Epidermal cells* slightly radially elongated (rectangular); those on both surfaces similar. Outer periclinal

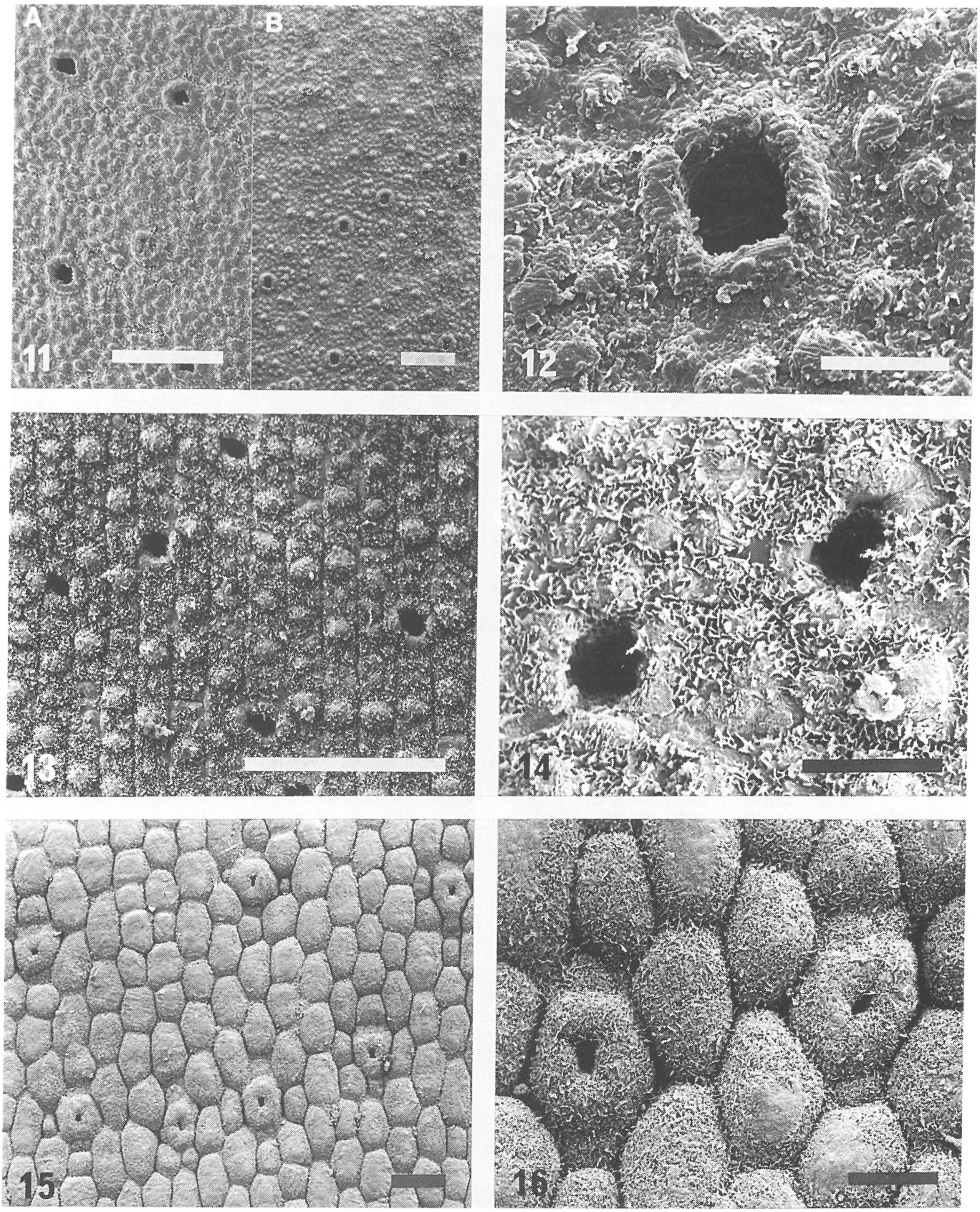
Table 2 Summary of salient, mainly leaf anatomical, differences between *Aloe bowiea, Chortolirion* and *Poellnitzia* (LM, light microscopy; SEM, scanning electron microscopy)

	Aloe bowiea	*Poellnitzia rubriflora*	*Chortolirion angolense*
Geographical distribution	endemic to Uitenhage district, eastern Cape	endemic to Robertson Karoo, south-western Cape	widespread in central southern Africa
Habitat	subtropical thicket	karroid shrublands	grassland
Habit	acaulescent, rosulate, leaf succulent	caulescent, rosulate, leaf succulent	bulbous plant; leaves weakly succulent
Leaf anatomy (transverse section; LM)			
Leaf outline	crescentiform	broadly triangular, keeled	broadly triangular
Cuticle	relatively thin	very thick	relatively thin
Cuticular lobes	consisting in part of epidermal cell wall		clear
Epidermal cells	periclinally elongated	radially elongated	
Outer periclinal epidermal cell walls	moderately cutinized	strongly cutinized	
Guard cell walls	evenly thickened	unevenly thickened	
Cuticular ledges	very short; with cell wall extensions	well-developed; without cell wall extensions	minute; unstained
Chlorenchyma	undifferentiated		differentiated into palisade and isodiametric cells
Vascular bundles	at boundary between chlorenchyma and central tissue		in central tissue
Phloem pole	T-shaped		single strand
Inner bundle sheath cap (parenchymatous)	large sectional area	absent	small sectional area
Sclerenchyma	absent	present at phloem pole; very large sectional area	absent
Central tissue	more or less sharply demarcated	merging with chlorenchyma	
Idioblasts	scattered in chlorenchyma		to inside of chlorenchyma
Leaf epidermis / surface (LM & SEM)			
Cuticular lobes	more or less upright	strongly overarching	more or less upright
Outline of epidermal cells	5- or 6-sided	predominantly 6-sided; leaf surface with "honeycomb" appearance	4-sided; longitudinally elongated
Outer periclinal epidermal cell walls	slightly convex; papillae generally absent	markedly domed; latter often grading into single papilla	plane; papillae present
Micropapillae	moderately coarse	absent	moderately coarse; coalescing adaxially



Figures 2 – 10 Details of transverse leaf sections in *Aloe bowiea* (2, 5, 8), *Chortolirion angolense* (3, 6, 9) and *Poellnitzia rubriflora* (4, 7, 10). Sources of material are given in Table 1. Sections of adaxial leaf segments (2 – 4), vascular bundles from mature leaves (5 - 7) and adaxial stomata (8 – 10) are shown. Adaxial leaf surfaces point towards the top of the page. Scale bars: 50 μm.

walls strongly cutinized (*ca.* 9 μm thick), others only slightly so; inner periclinal walls convex. Stomata sunken, suprastomatal cavity with parallel or slightly overarching lobes. Guard cell walls unevenly and heavily thickened, particularly towards supra- and substomatal cavities; inner cuticular ledges minute and darkly stained with PAS/TB,



Figures 11 – 16 Scanning electron micrographs of abaxial leaf surfaces of *Aloe bowiea* (11, 12), *Chortolirion angolense* (13, 14) and *Poellnitzia rubriflora* (15, 16). Sources of material are given in Table 1. Long axes of leaves are vertical throughout. Scale bars: 100 μm in Figures 11, 13 and 15, and 20 μm in Figures 12, 14 and 16.

outer ones minute and unstained. *Hypodermis* absent. *Chlorenchyma* 1 – 4-layered; cells thin-walled; present to inner sides of both surfaces, as well as the margins; cells of outermost layer strongly and regularly radially elongated, forming a distinct palisade layer; those of inner layer(s) more or less isodiametric. *Vascular bundles ca.* 10, evenly

distributed ab- and adaxially, arranged in a single ring, more or less equidistant from leaf surface and towards inside of chlorenchyma in central parenchymatous water storage tissue; bundles of alternating large and medium-sized ones; phloem poles directed outwards; no bundles distinctly positioned as 'keel' or marginal ones. *Phloem pole* represented by a single strand, parallel to outer leaf surface. Sieve tubes and companion cells very narrow; medium-sized bundles with few cells only. *Xylem* composed of few (1 – 4) tracheids of medium width. *Bundle sheaths* consisting of 1 – 2 well-defined layers of thin-walled parenchymatous cells; inner layer forming a small cap of parenchymatous cells at the phloem pole; sectional area of cap smaller than that of phloem and xylem together. *Sclerenchyma* absent. *Central tissue* composed of large, nearly isodiametric parenchymatous cells; merging rather imperceptibly with chlorenchyma. *Crystals* present as raphide bundles in scattered idioblasts immediately to the inside of the chlorenchyma; not specifically associated with vascular bundles. *Silica bodies* and *tannins* not observed.

Leaf epidermis/surface, LM & SEM

Stomata anomocytic, sunken; lobes almost upright, fused; outer pore more or less square. *Primary sculpturing*: epidermal cells 4-sided; longitudinally elongated (rectangular), or slightly fusiform; longitudinal radial walls distinctly depressed; transverse radial walls obscure. *Secondary sculpturing*: outer periclinal walls of epidermal cells plane; papillae 2 – 4, serially (longitudinally) arranged on each cell of the abaxial surface; adaxially absent. *Tertiary sculpturing*: micropapillae moderately coarse, many per cell and distributed over entire surface, adaxially coalescing to form low, transverse, ridge-like structures; micropapillae on subsidiary cells more prominent. *Wax* present as amorphous deposits over entire leaf surface, partly blocking some stomata.

Poellnitzia rubriflora (Figures 1C, 4, 7, 10, 15 and 16)

Leaf in transverse section, LM

Outline broadly triangular in transverse section, occasionally with an incomplete, obliquely-situated abaxial keel; adaxial surface plane or slightly concave; abaxial surface convex; margins acute, scabrid. *Cuticle* very thick (up to 70 μm), following outline of outer wall of epidermal cells. Outer part clear, inner part apparently slightly grading with outer-most part of epidermal cell wall. Lobes forming the suprastomatal cavity well developed, with wall of subsidiary cell extending slightly into lobe. *Epidermal cells* radially elongated and distinctly papillate (strongly convex); those on both surfaces similar. Outer periclinal walls strongly cutinized (up to 20 μm thick), others only slightly so, or not at all. *Stomata* sunken, suprastomatal cavity with strongly overarching lobes. Guard cell walls unevenly and strongly thickened, particularly the exposed walls; outer and inner cuticular ledges present, without cell wall extensions, hence appearing unstained with PAS/TB. *Hypodermis* absent. *Chlorenchyma* usually multi-layered; present to inner sides of both surfaces, though better developed abaxially; cells more or less isodiametric, not palisade-like. *Vascular bundles* relatively large and more numerous abaxially (*ca.* 10), smaller and fewer (*ca.* 4) adaxially; more or less equidistant from leaf surface and on boundary between chlorenchyma and central parenchymatous tissue; phloem poles directed outwards; no bundles distinctly positioned as 'keel' or marginal ones. *Phloem pole* more or less T-shaped in outline, the stalk of the T directed outwards. Sieve tubes and companion cells very narrow. *Xylem* composed of usually 1 – 5 tracheids of small diameter. *Bundle sheath(s)* consisting of 1 or 2 layers of thin-walled parenchymatous cells; outer layer usually clearly distinguishable from surrounding cells. Bundle caps of large thin-walled cells absent. *Sclerenchyma* present as a well-developed cap (more or less reniform in transverse section) at the phloem pole; sectional area of cap much larger than xylem and phloem together. *Central tissue* composed of large parenchymatous cells, merging imperceptibly with chlorenchyma. *Crystals* present as raphide bundles in idioblasts; relatively few and mainly confined to the chlorenchyma on the adaxial side; not specifically associated with vascular bundles. *Silica bodies* and *tannins* not observed.

Leaf epidermis/surface, LM & SEM

Stomata anomocytic, sunken; lobes strongly overarching, fused; outer pore minute, square or rectangular. *Primary sculpturing*: epidermal cells (4-) 6-sided in surface view, resulting in a marked 'honeycomb' appearance; anticlinal cell walls distinctly grooved. *Secondary sculpturing*: outer periclinal walls of epidermal cells markedly domed, the latter often grading into a single papilla. *Tertiary sculpturing*: micropapillae absent. *Wax* present as amorphous deposits over entire leaf surface, partly blocking some stomata.

Discussion and Conclusions

This investigation of the leaf anatomy of *Chortolirion*, *Poellnitzia* and *Aloe bowiea* has revealed some characters which may be of diagnostic and probably also taxonomic value. The more significant of these are the presence of chlorenchymatous tissue distinctly differentiated into a palisade layer and isodiametric cells, the inner bundle sheath cap-type, the localization of crystalliferous idioblasts, the degree of cutinization of the epidermal cell wall, and leaf surface patterns. These and other leaf anatomical aspects of representatives of the Alooideae are discussed below. A comparison of the taxa under consideration to other alooid genera and *Kniphofia* with regard to selected leaf anatomical characters is given in Table 3.

Chlorenchyma

Of all the Alooideae taxa of which leaf transverse sections have been investigated to date, only *Chortolirion* displays chlorenchymatous tissue which is distinctly differentiated into a palisade layer (a single layer of radially elongated cells present adjacent to both the upper and lower surfaces) and more or less isodiametric (spongy) cells (see footnote to Table 3 for references). Since the arrangement of cells in the chlorenchyma is under strong genetical control, this is considered a diagnostic character for *Chortolirion*. There is, however, a need for more, wide-ranging studies on leaf structure in the Alooideae, especially on the graminoid-leaved species of *Aloe* and *Haworthia* (*cf.* Schneider 1972).

Inner bundle sheath caps

This character has been extensively reviewed by Beaumont *et al.* (1985) and is not discussed in detail here. However, to date the internal structure of *Chortolirion* leaves had not been investigated microscopically (see Table 1 in Beaumont *et al.* 1985). The present study showed that this genus, in common with most other alooid taxa, including *Aloe bowiea*, has an inner bundle sheath cap consisting of thin-walled parenchymatous cells only. In contrast, the bundle sheath caps of *Poellnitzia* are large (sectional area), reniform, and sclerenchymatous. The parenchymatous state is generally regarded as derived since it is a unique feature in an otherwise advanced group of plants (Beaumont *et al.* 1985; Smith & Van Wyk 1991).

Localization of crystalliferous idioblasts

Very little is known about the localization of crystalliferous idioblasts in the leaves of representatives of the Alooideae, and the type(s) of crystals that they contain. For *Chortolirion* (Table 2), idioblasts have not been found in the chlorenchyma, whereas, in the case of *Poellnitzia* and *Aloe bowiea*, they occur scattered in the chlorenchyma. This character, too, requires more detailed investigation in a representative sample of alooid taxa.

Cutinized epidermal cell walls

Although strongly cutinized outer periclinal cell walls are not unique to the Alooideae, the presence of this type of wall structure among the genera *Astroloba, Chortolirion, Gasteria, Haworthia* and *Poellnitzia* might be phylogenetically significant (Cutler 1972). Although Baijnath (1980) did not mention this character when he investigated the leaf anatomy of *Kniphofia* Moench, reference to his Figures 2A and 2C indicates its presence in at least some species of the genus.

In a leaf anatomical study of the monocotyledonous *Gloriosa superba* L., *Littonia modesta* Hook., *Sandersonia aurantiaca* Hook. and *Hexacyrtis dickiana* Dint. (Iphigenieae: Colchicaceae), Baijnath (1988) found markedly thickened outer periclinal epidermal cell walls in *Hexacyrtis* only. Significantly, Baijnath (1988) suggested a correlation between the leaf anatomical characters of these species and their growth forms and habitats. As would be expected, *H. dickiana*, a species from arid sandy places in the Namib Desert, shares a number of anatomical features with xerophytes (see also Cutler 1978b, 1982, on the correlation between leaf surface sculpturing and habitat in *Aloe* and in general).

Leaf surface sculpturing

The leaf surface sculpturing of *Chortolirion angolense* has previously been investigated by Cutler (1979; *Haworthia angolense* Baker). However, our results differ from those of Cutler (1979) in a number of respects. For example, we found the cuticular lobes to be fused (not free), the outline of the suprastomatal chamber to be square (not rectangular), the micropapillae coalescing adaxially to form transverse ridges (not well-spaced), at least the longitudinal radial walls distinctly depressed (not indistinct), and the wax present as amorphous deposits (not flaky particles). These discrepancies show that considerable variation exists in the leaf surface patterns of this aberrant monotype. Clearly, any taxonomic changes proposed for a particular taxon on the basis of leaf anatomy alone should be based on a representative range of samples.

Previous SEM work on leaves of the Alooideae has focused mainly on the surface sculpturing of the adaxial epidermis. The present study indicated different infraspecific patterning on the ad- and abaxial leaf surfaces of some samples, especially in the case of *Chortolirion* and *Aloe bowiea* (Kariega specimen). This emphasizes the need for future routine examination of both leaf surfaces. Furthermore, some infraspecific variation exists in the abaxial leaf surface patterning of specimens of *A. bowiea* collected from different localities (Figure 11A: Coega *vs* Figure 11B: Kariega). The 'honeycomb' patterning on both the ad- and abaxial leaf surfaces of *Poellnitzia* is very distinctive and should serve to characterize the genus on leaf anatomical grounds alone. It is quite unlike any pattern previously recorded for a member of the Alooideae.

Stomata

The leaves of all the species studied are amphistomatic with the guard cells very deeply sunken, and more or less overarched by prominent cuticular lobes. In addition, the guard cells also have inner and outer cuticular ledges which may (*Aloe bowiea*; Figure 8) or may not (*Chortolirion, Poellnitzia*; Figures 9 and 10) contain cell wall extensions. Thus, two extensions of the stomatal pore are delimited: a front (outer) cavity and a back (inner) cavity (Stace 1965).

Morphologically, stomata of the Alooideae have previously been considered tetracytic (four subsidiary cells; two polar and two lateral) (Cutler 1972). However, the present authors are not convinced that the epidermal cells bordering the guard cells are that different from the epidermal cells which are not in direct contact with guard cells, to warrant referring to them as subsidiary cells. Pending ontogenetic studies of Alooideae stomata, these structures are best referred to as anomocytic. Although in many alooid taxa the cells bordering the guard cell pair are furnished with distinctive micropapillae and/or conspicuous lobes, morphologically similar stomatal types can be developmentally dissimilar. Such non-homologous characters obviously cannot be used to signify affinity, since different genetic mechanisms are involved (Tomlinson 1974; Patel 1978).

It is noteworthy that, as is the case with cuticle and epidermal cell wall thickness (Cutler 1978b), stomatal elevation (sunken *vs* superficial) is not a reliable indication of xeromorphy, habitat or climate. For example, Eggli (1984) has shown that in most cases in the highly succulent Cactaceae, the stomata are superficial (but see Barthlott 1990 on ecological aspects of surface sculpturing).

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